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Population Characteristics and Nomenclature of the Hermit Thrush

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My interest in the geographical variation in the hermit thrush, *Catharus* (=*Hylocichla*) *guttatus*, was aroused while investigating marked differences among populations of the Pacific Northwest (Jewett, Taylor, Shaw, and Aldrich, 1953). Since that time I have examined specimens from the entire range of the species that seem to give a somewhat different picture of the subspecific relationships from that of my previous arrangement as well as from that of the most recent previous revision (Phillips, 1962) and such recent standard manuals as "American Ornithologists' Union" (1957) and Ripley (1964).

Many of the specimens utilized in the study are in the U.S. National Museum, but a considerable number were borrowed from other institutions. For the loan of critical material I am indebted to the curators of the following collections: Museum of Comparative Zoology, Harvard University; National Museum of Canada; Cleveland Museum of Natural History; British Columbia Provincial Museum; Museum of Vertebrate Zoology, University of California; Field Museum of Natural History, H. H. Bailey Collection; Ira N. Gabrielson Collection; San Diego Natural History Museum; Charles R. Conner Museum, Washington State University; Museum of Zoology, University of Utah; Museum of Zoology, University of Michigan; University of Alaska; American Museum of Natural History; Washington State Museum, University of Washington; Collection of Alex Walker; and Denver Museum of Natural History.

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Statistical reliability of the measurement differences recognized in this paper was determined by Robert Heath, Bio-statistician of the Bureau of Sport Fisheries and Wildlife.

Geographical and Ecological Distribution

The hermit thrush is one of the most widely distributed migratory birds in North America. Its breeding range is extensive, including most of the boreal and mountainous coniferous forest areas of the continent north of Mexico. There is no good evidence that the species breeds south of the United States-Mexican border. Summer specimens collected in the Sierra de la Laguna, Baja California, were regarded by Brewster (1902) and Grinnell (1928) as indicating breeding, but McCabe and McCabe (1932) and Banks (1967) seem to be justified in considering them migrants or at most nonbreeding birds. In migration, hermit thrushes move southward and spread out to winter over most of the southern portion of the United States and through Mexico to Guatemala.

The hermit thrush breeds in all or part of seven major ecological climax zones or "Life Areas" delineated by Aldrich (1963, p. 532). These include all of the region characterized by the transcontinental "Closed Boreal" forest from Newfoundland to northern British Columbia and central Alaska, the more southern "Northern Hardwood-Conifer" area from Nova Scotia to Minnesota and southeastern Manitoba, southward in the Appalachian Mountains to West Virginia, and the "Aspen Parkland" from central Manitoba and northwestern Minnesota west to central and central-southern Alberta. The small breeding populations on Long Island, N.Y., and Cape Cod, Mass., in the pine barrens section of the "Eastern Deciduous" Life Area are probably relicts of a former more favorable ecological situation. The hermit thrush breeds also, at least locally, in the more northern, transcontinental "Open Boreal" forest area that extends from Labrador to western Alaska. In the western part of the continent it nests in high mountain forest zones with climax vegetation of a coniferous or mixed coniferous-deciduous life form, particularly the "Closed Boreal" (subalpine) and "Montane Woodland-Brush," from interior British Columbia south to southern California, Arizona, New Mexico, and extreme western Texas. Along the Pacific coast it breeds in the lowland and coastal mountain "Pacific Rain Forest" zone from California northward to the coast of southern Alaska and westward to the base of the Alaska Peninsula and Kodiak Island. Westward on the Alaska Peninsula it nests in alders beyond the limit of large trees in the "Arctic-Alpine" area (Murie, 1959).

Within these geographically extensive "Life Areas," each characterized by a single ecological climax type, the hermit thrush nests

in a variety of habitats ranging from dense coniferous forest to low deciduous shrubs. It is primarily, however, a bird of somewhat open situations in a generally forested area such as brushy thickets along roadsides or forest borders, partly open bogs, and young mixed coniferous-deciduous growth that has sprung up after a forest has been cut or burned.

In winter the habitat is usually a dense cover of woody growth such as pine forests with brushy undergrowth or brushy swamps in the southeastern United States and chaparral and streamside thickets in the Southwest.

Trends in Morphological Variation

Morphological variation of the hermit thrush was determined by comparison of 2039 study specimens. Of these, 524 were adults collected during the breeding season in virtually all sections of the breeding range of the species. The other 1515 specimens were adults taken during migration and wintering seasons or were juveniles collected on the breeding grounds.

The adult plumages of the hermit thrush are derived from a single basic plumage grown after a postjuvenal or postnuptial (prebasic) molt that takes place in the late summer. The fall plumage, therefore, consists of freshly grown feathers while the nuptial plumage of late spring and early summer is derived gradually by wear from these same feathers.

For the study of geographic variation in size and color, I have relied entirely on adult specimens taken during the breeding season. Identification of specimens in fresh autumn plumage was made by using the same relative differences in color determined from more or less worn breeding specimens. I realize that discrimination of both color and length of wing and tail would be more exact if based entirely on specimens in fresh postnuptial or postjuvenal plumage. In my opinion, however, individuals that have molted into fresh plumage, particularly young of the year, cannot safely be assumed to be on their breeding grounds. Evidence of postbreeding wandering by many species is coming to light more and more often. A good example has been documented in the white-crowned sparrow (DeWolfe, 1967). A number of apparent cases were noted during the present hermit thrush study. T. D. Burleigh (in litt.) informs me that he has recorded fall migrant hermit thrushes at Moscow, Idaho, as early as September 4. Phillips et al. (1964) record *C. g. sequoiensis* at San Francisco Peaks, Ariz., on September 1. They also found a specimen of *C. g. auduboni* away from the breeding grounds at Flagstaff, Ariz., in August and interpreted its presence as representing postfledgling dispersal of young.

The specimen study showed the hermit thrush to be quite variable in size and color. Within any given breeding population, male hermit thrushes average larger, and in most cases significantly larger, than females in wing length (fig. 1). On the other hand, the bills of females tend to be equal to or longer than those of males (fig. 2). When shown as a ratio, the relatively longer bills of females in proportion to wing

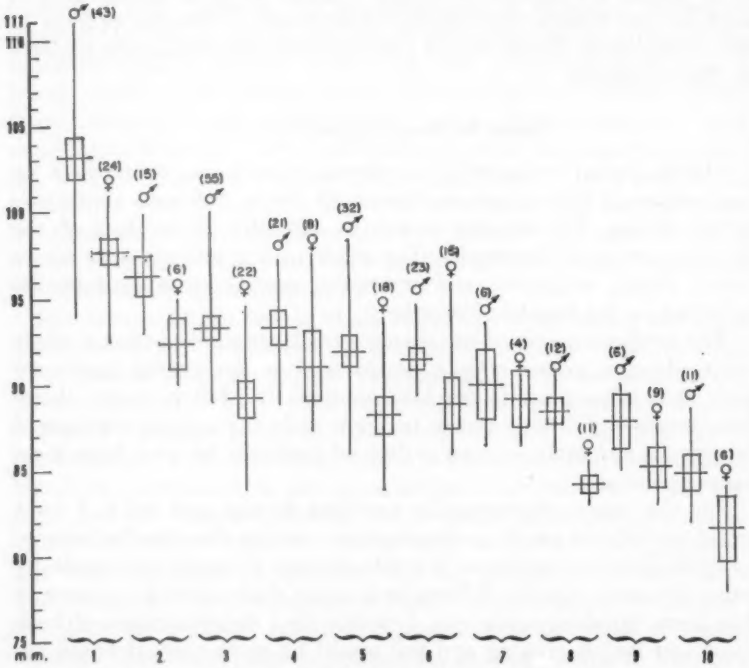

FIGURE 1.—Wing lengths of subspecies of *Catharus guttatus*, showing ranges (vertical lines), means (horizontal), and two standard errors on either side of the means (rectangles). (Numbers in parens=sample sizes. Numbers at bottom=1, *auduboni*; 2, *sequoiensis*; 3, *faxoni*; 4, *euborius*; 5, *crymophilus*; 6, *oromelus*; 7, *vaccinius*; 8, *guttatus*; 9, *nanus*; 10, *slevini*.)

length becomes more apparent (table 1). In nine out of 10 populations, female specimens have proportionately longer bills on the average than males. Within any given breeding population, no differences in color correlated with sex were detected. There are two slightly differentiated color phases (rufescent and grayish) that may appear in any population (Oberholser, 1932). In the present study these phases, noted in all populations, seemed to be most distinct among eastern birds. The speckled dorsal plumage of juveniles is quite dif-

ferent from the uniformly colored upper parts of adults. Some of the speckled juvenal feathers among the upper wing coverts are carried over after the postjuvenal molt, even into the following breeding season, making possible the recognition of first-year birds up to the time of the first postnuptial molt. This subadult plumage (with the scattered juvenal feathers among the wing coverts) is very slightly more rufescent and paler on the average than the fully adult plumage when equivalent color phases of each are compared in series. Wear of

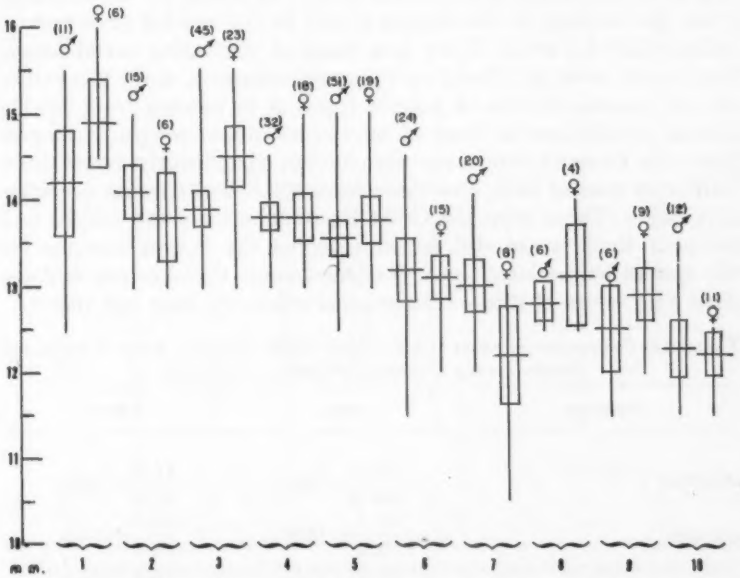

FIGURE 2.—Bill lengths of subspecies of *Catharus guttatus*, showing ranges (vertical lines), means (horizontal), and two standard errors on either side of the means (rectangles). (Numbers in parens = sample sizes. Numbers at bottom = 1, *slevini*; 2, *sequoiensis*; 3, *auduboni*; 4, *crymophilus*; 5, *faxoni*; 6, *oromelus*; 7, *euborius*; 8, *vaccinius*; 9, *nanus*; 10, *guttatus*.)

feathers causes color to be duller, more grayish, and sometimes paler in the breeding season than in fresh autumn plumage.

Although McCabe and McCabe (1932) minimized the reliability of color characters in distinguishing populations of hermit thrushes, specimens taken at the same season of the year reveal marked geographical differences in color (shade and hue) that are far greater than the differences due to age or color phase. East of the Rocky Mountains, color of breeding birds is relatively uniform over a vast area, but west the of Rockies, particularly along the coast, much geographical variation occurs in a relatively limited area, and changes

between extremes are quite sharp. Trends in geographical variation of the hermit thrush indicated by Ridgway's (1907) detailed descriptions of subspecies recognized at that time agree in general with findings of the present study.

If we assume that wing length is an indicator of overall size of hermit thrushes—and studies by McCabe and McCabe (1932) indicate that it is—the smallest birds breed in the immediate vicinity of the Pacific Coast. On the other hand, the bill lengths of birds in this area, correlated with distribution from north to south, range from the smallest to the largest found in the species (averages of males 12.2–15.6 mm). There is a trend of decreasing tarsal length from north to south. Based on wing measurements, there is a rather abrupt increase in size of hermit thrushes in passing from Pacific coastal populations to those of interior mountain ranges. Examples from the Cascade range are slightly but significantly larger than California coastal birds and those from the Sierra Nevada considerably larger. Those from the Great Basin mountains and middle and southern Rockies are still larger, reaching the largest extreme for the species in the latter area. Eastern hermit thrushes are uniform sized with wings of medium length and relatively long legs (fig. 3).

TABLE 1.—*Comparison of ratios of bill to wing length* (culmen: wing) *in males and females among subspecies of* Catharus guttatus

Subspecies	Male	Female
auduboni	$\frac{14.0}{101.6}=.1377$	$\frac{14.4}{97.2}=.1481$
guttatus	$\frac{12.3}{88.5}=.1389$	$\frac{12.2}{84.2}=.1448$
euborius	$\frac{13.0}{93.4}=.1391$	$\frac{12.2}{91.2}=.1337$
vaccinius	$\frac{12.8}{90.0}=.1422$	$\frac{13.1}{89.4}=.1465$
nanus	$\frac{12.5}{87.9}=.1425$	$\frac{12.9}{85.1}=.1515$
oromelus	$\frac{13.2}{91.6}=.1441$	$\frac{13.1}{88.9}=.1473$
faxoni	$\frac{13.6}{93.5}=.1454$	$\frac{13.8}{89.2}=.1547$
sequoiensis	$\frac{14.1}{96.4}=.1462$	$\frac{13.8}{92.5}=.1491$
crymophilus	$\frac{13.8}{92.1}=.1498$	$\frac{13.8}{88.3}=.1562$
slevini	$\frac{14.2}{84.8}=.1674$	$\frac{14.9}{81.7}=.1823$

In color the greatest variation occurs in the Pacific Northwest. The most darkly colored birds appear on Vancouver and the Queen Charlotte Islands off the coast of British Columbia and the palest in the interior of that province as well as the vicinity of the California coast. The extreme in grayness is reached by populations in northern Idaho and central southern British Columbia, and one of the most reddish occurs on the Queen Charlotte Islands. All of these extremes in color are found in the smaller winged group of hermit thrushes (fig. 4).

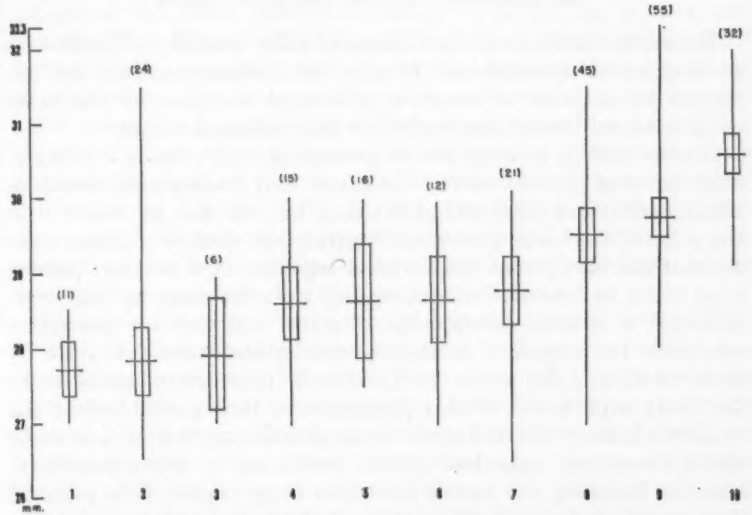

FIGURE 3.—Male tarus lengths of subspecies of *Catharus guttatus*, showing ranges (vertical lines), means (horizontal), and two standard errors on either side of the means (rectangles). (Numbers in parens=sample sizes. Numbers at bottom=1, *slevini*; 2, *oromelus*; 3, *vacciniius*; 4, *sequoiensis*; 5, *nanus*; 6, *guttatus*; 7, *euborius*; 8, *auduboni*; 9, *faxoni*; 10, *crymophilus*.)

In the north, the transition from the small-winged Pacific coastal populations to the medium-sized eastern birds occurs almost immediately after leaving the coast. Examples from interior Alaska, Yukon, and interior northern British Columbia are larger and paler than the coastal birds. From there eastward there is a change to darker coloration with more rufescent upper parts and flanks, and to relatively long legs. Transition in these characters occurs in western Alberta. Birds from south-central Mackenzie (Great Slave Lake), northeastern Alberta, and Saskatchewan east to the Atlantic seaboard are relatively uniformly colored on upper parts and flanks. The only distinct geographical trend in coloration of this thrush in

the eastern parts of its range is a darkening of the pigmentation of the upper parts in the northeast.

In the south, transition from the very small birds of the California coast to the large type of the Great Basin and southern Rockies is quite abrupt through intermediate populations of the Sierra Nevada and Cascades. Color change is a relatively slight darkening above and an increase in both number and darkness of ventral spots progressing from west to east in this area.

Morphological Variation and Environment

References to apparent correlation of color intensity of birds with environmental moisture and of size with temperature are too numerous to mention although experimental evidence of the exact environmental factors responsible for the variations is rare.

Bowers (1960), in a significant pioneering study, found a relationship between environmental moisture and background color of wrentit (*Chamaea fasciata*) habitat that, in turn, was correlated with the color of the birds' plumage. The fact that wrentit plumage color and habitat background color varied together, in a gradient passing from moist to drier environments away from the coast in California, indicated a definite relationship. Natural selection for protective coloration by predation, as shown experimentally for deer mice by Dice (1947) and for moths by Kettlewell (1955, 1956), seems to be the likely explanation of this phenomenon. It is probable that the evidently indirect effect of environmental moisture on color is brought about by natural selection through predation in many species of animals, including the hermit thrush to some degree. It is assumed that cryptic coloration, if it exists in hermit thrushes, should be judged on the basis of general resemblance to the forest floor or very low vegetation since this species nests and spends most of its time on or near the ground (Bent, 1949). Thus, general tone of leaf and twig litter on the forest floor would be significant. Moisture would affect the shade of the litter and humus, and density of the understory would control the amount and quality of light reaching the ground; therefore, as Bowers (1960) suggests, the general background tone in vegetated environments is darker in moist climates and paler in arid regions. Other important observations on the correlation of bird plumage coloration with habitat backgrounds include: Moreau (1930), Behle (1942), Davis (1951), Meinertzhagen (1950), and Selander (1954).

McCabe and McCabe (1932) and Munro and Cowan (1947) have commented on the general correlation of variation in hermit thrushes with environment in the Northwest. Certainly both the morphology

of the birds and environmental conditions vary more markedly there than anywhere else within the breeding range of this species.

In the redwood section of the "Pacific Rain Forest" belt along the coast of California and southwestern Oregon, as delineated by Schantz and Zon (1924) and Küchler (1964), occurs a very small, pale hermit thrush with a large bill. This is sharply distinct from larger, relatively small-billed and darker populations from the adjoining mountain forests of the Cascades and the very much larger, although similarly colored, birds of the adjoining mountain forests of the Sierra Nevada. Thrushes from varying types of the "Pacific Rain Forest" (Halliday, 1937; Rowe, 1959; Küchler, 1964) further north are slightly larger in wing and tarsus than those from the California coast, have smaller bills, and break down into several color variants, all quite distinct from the California coastal birds. Thus, there is no uniform color type—conforming to Gloger's rule—characterizing the very moist "Pacific Rain Forest" as a whole, as delineated by Aldrich (1963). Rather, the hermit thrushes of this zone, relatively uniform ecologically, exhibit the extremes in color variation found in the species—from almost the most reddish to the most grayish and from the darkest to the palest.

Specimens from the Pacific coastal belt also exhibit the extremes in bill size. The only characters they seem to possess in common are small measurements of structures other than bill. These birds are correlated with a milder coastal climate and, if indicative of body mass as McCabe and McCabe (1932) found to be the case in wings of hermit thrushes, they are in accordance with Bergmann's rule. Pitelka (1951) found a similar situation in the variation of scrub jays. An exception to Bergmann's rule would seem to be the small size of hermit thrushes in the high interior mountains of southern British Columbia and northern Idaho.

The relatively large bill of the more southern Pacific coastal population is in conformance with Allen's rule although the length of legs does not follow this rule. The longest legs are found in eastern populations but, contrary to Allen's rule, the northernmost ones have longer legs than those from farther south. This is also the trend on the Pacific Coast.

Except for the coastal population from California north to Washington, there appears to be a correlation in the dark color tone of the plumage of hermit thrushes from the humid coastal area as compared with the paler shade found in those from more interior mountains. Thus, the grayish trend exhibited by birds of southern British Columbia has its darkest expression in the rain forests of Vancouver Island, while the more rufescent birds of northern British Columbia and Alaska reach the peak of darkness on the extremely

wet offshore islands of northern British Columbia and southeastern Alaska. In the opposite direction, the grayish populations of the relatively moist cedar-hemlock-pine "Columbian Forest," a disjunct of the "Pacific Rain Forest," on the west side of the Rockies in southern British Columbia and northern Idaho, become paler in the relatively dry mountain coniferous forests to the north, east, and south

Progressing eastward from the relatively dry Rocky Mountain forests through the moister and fairly uniform boreal forests of eastern Canada, the color of hermit thrushes becomes more rufescent and slightly darker immediately upon departure from the Rocky Mountains. Further darkening occurs when we reach the eastern part of the "Closed Boreal" forest east of James Bay in Quebec and Newfoundland. The darker pigmentation in this northeastern part of the species' range is correlated to some extent with the "Closed Boreal" forest as distinguished from the "Northern-Hardwood-Conifer" area that comprises the southeastern part of its range. This correlation, however, is far from complete because west of James Bay and Lake Mistassini, Quebec, the morphological differences correlated with these two ecological zones disappear. It is possible that habitat background values vary from one association to another within the boreal forest belt to supply the basis for selection. The darker coloration is correlated roughly with sections of the "Closed Boreal" area that Halliday (1937) called the "Northeastern Coniferous Section," the "Gaspé Section," the "East James Bay Section," and the "Hamilton-Ungava Valleys Section." These sections agree in having relatively deep, well-drained soils and are characterized by upland forests of a relatively luxuriant growth of large trees, chiefly black spruce and balsam fir. Forest sections to the west, starting with the "Central Laurentian Section" and the "Northern Clay Section" of Halliday (1937), have either sandy or poorly drained soils that support forests of more stunted or open type, chiefly of black spruce, jack pine, aspen, balsam-poplar, and white birch. These differences in forest growth type conceivably could produce color and light differences of the substratum that would be the basis for differential selection in darker and lighter colored hermit thrushes. However this may be, the reason why the birds of the "Northern Hardwood-Conifer" area are closer to the western "Closed Boreal" forest sections than to the eastern is not evident. As far as is known, the winter environments of the two differing eastern populations are similar.

Although there are a few apparent discrepancies, there appear to be certain correlations between climax forest type of breeding areas and colors of plumages in the western part of the continent. There, all the darkest types are in the moist areas of the Pacific Northwest.

All of the pale types (with the exception of the California to Washington coastal population) are from the relatively dry interior mountain forests. All of the small types are along the humid Pacific Coast or almost equally moist coastal mountains and west slopes of the Rockies in southern British Columbia and northern Idaho. On the other hand, the largest types are from the higher and drier mountain forest of the interior.

The large interior birds, although individually quite variable, show surprisingly little average variation either in size or color over vast areas despite the extremely discontinuous distribution of their mountain coniferous summer home. Suitable breeding habitat frequently is broken up into many "islands" sometimes separated by wide expanses of desert. Such disruptions of populations might be expected to offer much more of an obstacle to gene flow than the contiguous areas of different ecological climax type that support quite different appearing populations in the vicinity of the Pacific Coast. Evidence seems to support a greater importance of adaptation to environmental conditions than of physiographic or ecological barriers to gene flow in the development of present morphological differences in hermit thrushes. On the other hand, isolation on Vancouver and Queen Charlotte Islands may have reinforced the trend toward dark pigmentation of birds adapted to moist forest conditions along the northwest coast.

Another fact, indicated by Grinnell (1901), that may bear on the seeming greater effect of moist habitat on the color of the Vancouver and Queen Charlotte Islands birds is that they are less migratory than other populations and winter chiefly along the Pacific Coast in habitats similar to those in which they breed. Thus, they are exposed to habitat conditions associated with a humid climate throughout the entire year. On the other hand, the paler populations of the Pacific Coast south of the Canadian border and those of the interior mountains are less restricted in migration and winter to a large extent in relatively arid environments of the southwestern United States and Mexico. Thus, there is an opportunity for an entirely different set of selection factors to operate on these populations in winter, and these may be more critical to survival of paler individuals than factors encountered on the breeding grounds, as suggested by Salomonsen (1955) for certain other species.

It would seem that the hermit thrush, which breeds in a variety of habitats located in at least seven "Life Areas," each characterized by different climatic climax types, is a racially variable species. This variation might be expected since the hermit thrush has become adapted to many different environments, a response that Miller (1956) has pointed out is conducive to intraspecific variability. In some

instances the variable characters are in agreement with obvious environmental conditions on the breeding grounds and in accordance with the classical Gloger's, Bergmann's, and Allen's rules.

The numerous exceptions probably are accounted for by adaptation to critical environmental conditions encountered by these populations while in migration or on their wintering grounds. Such exceptions have been documented frequently for intensively studied species such as the juncos (Miller, 1941b), vireos (Hamilton, 1958), and white-crowned sparrows (Banks, 1964).

Characteristics and Nomenclature of Populations

The generally accepted name for the hermit thrush has been *Hylocichla guttata* (Pallas) (type-locality: Kodiak Island, Alaska) since the American Ornithologists' Union (1902) decided that the previously accepted name, *Hylocichla aonalaschkae* (Gmelin), was based on an unidentifiable description.

Inclusion of the hermit thrush in the genus *Catharus* is based on evidence presented by Ripley (1952) and Dilger (1956). There are rather marked morphological differences between most of the Neotropical members of the group originally separated in the genus *Catharus* and the North American species that previously have been included in the genus *Hylocichla*. These differences include relatively long leg bones, short rounded wing with relatively long tenth primary, small sternum, brightly colored eye ring and bill in the tropical group. These differences, however, are not as pronounced in some of the more northern members of the tropical group. As Dilger (1956) has pointed out, all members of the genus *Hylocichla*, except *H. mustelina*, are more like *Catharus*, while the wood thrush is more like *Turdus*. The relationships of *H. mustelina* to *Turdus* noted by Dilger were in aggressive display, nest construction, and serological resemblance. In addition, I have noted that certain skull characters, particularly a deep groove above the auditory bulla for the attachment of the aductor mandibulae muscle, are present in typical members of genus *Turdus* and to a lesser extent in *H. mustelina* but which are quite indistinct in other species of *Hylocichla* and *Catharus*. Everything considered, there appear to be sufficient resemblances and overlap of characters to warrant placing all species that have been grouped in the genus *Hylocichla*, except *H. mustelina*, in the genus *Catharus*, and equally good reasons for not including *H. mustelina* in this genus. Since the wood thrush is the type-species of *Hylocichla*, this probably should be maintained as a monotypic genus, as Dilger (1956) has suggested, until such time as its relationships are better understood.

In previous sections of this paper it has been noted that color and size were associated during the breeding season with particular geographical areas and, to a large extent, with particular sets of ecological conditions. The differences in certain groupings of characters appear to be sufficiently distinct morphologically, ecologically, and geographically to permit recognition of the populations possessing them as different subspecies (fig. 4).

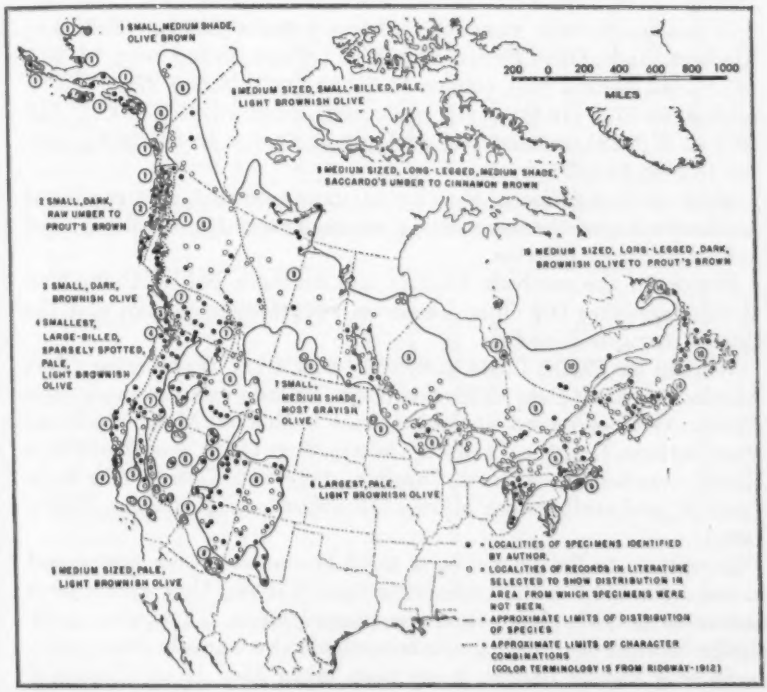
1 SMALL, MEDIUM SHADE, OLIVE BROWN
2 SMALL, DARK, RAW UMBER TO PROUT'S BROWN
3 SMALL, DARK, BROWNISH OLIVE
4 SMALLEST, LARGE-BILLED, SPARSELY SPOTTED, PALE, LIGHT BROWNISH OLIVE
5 MEDIUM SIZED, SMALL-BILLED, PALE, LIGHT BROWNISH OLIVE
6 MEDIUM SIZED, LONG-LEGGED, MEDIUM SHADE, SACCARDO'S UMBER TO CINNAMON BROWN
7 SMALL, MEDIUM SHADE, MOST GRAYISH OLIVE
8 LARGEST, PALE, LIGHT BROWNISH OLIVE
9 MEDIUM SIZED, PALE, LIGHT BROWNISH OLIVE
10 MEDIUM SIZED, LONG-LEGGED, DARK, BROWNISH OLIVE TO PROUT'S BROWN
200 0 200 400 600 800 1000
MILES
• = LOCALITIES OF SPECIMENS IDENTIFIED BY AUTHOR.
○ = LOCALITIES OF RECORDS IN LITERATURE SELECTED TO SHOW DISTRIBUTION IN AREA FROM WHICH SPECIMENS WERE NOT SEEN.
— = APPROXIMATE LIMITS OF DISTRIBUTION OF SPECIES
···· = APPROXIMATE LIMITS OF CHARACTER COMBINATIONS
(COLOR TERMINOLOGY IS FROM RIDGWAY-1912)

FIGURE 4.—Breeding distribution and morphological variation in subspecies of *Catharus guttatus* (1=*guttatus;* 2=*nanus;* 3=*vaccinius;* 4=*slevini;* 5=*sequoiensis;* 6=*audubonii* 7=*oromelus;* 8=*euborius;* 9=*faxoni;* 10=*crymophilus*).

All of these populations have previously supplied names based on adequate descriptions. These are characterized under the oldest names available for them in the following descriptions. Unless otherwise specified, color designations are for the back, wings, and crown (not upper tail coverts and tail). Capitalized color terms are those of Ridgway (1912). Numbers preceding the name refer to the position of the populations' distribution on the map (fig. 4). Measurements (extremes and means) are in millimeters. They include the wing

(chord of unflattened wing), tail (from insertion of two central tail feathers), culmen (exposed portion), tarsus, and middle toe (without claw). Comparisons of means of wing, culmen and tarsus measurements are given in tables 2 to 7 and their ranges, means, and two standard errors are shown in figures 1 to 3. Gradation of races by wing, tail, bill, and tarsus length and by shade and hue of color is shown in table 8. Breeding, migration, and winter distribution is based almost entirely on determination of specimens examined in the present study.

1. ALASKA HERMIT THRUSH: *Catharus guttatus guttatus* (Pallas).—Medium shade. Olive Brown. Small: ♂ (12 specimens), wing 86–90.5 (88.5), tail 61–68.5 (65), culmen 11.5–13.5 (12.3), tarsus 27–30 (28.7), midtoe 16–17.5 (16.5); ♀ (11 specimens) wing 83–85.5 (84.2), tail 59.5–65.6 (63.2), culmen 11.5–12.5 (12.2), tarsus 27–29 (28.3), midtoe 15.5–16.5 (16.2).

Paler and less rufescent than *nanus;* more rufescent, shorter winged and longer legged than *oromelus;* paler than *vaccinius;* smaller winged and darker than *euborius.*

Breeds on the southern Alaskan and northern British Columbian coasts, excluding the outer islands of southeastern Alaska and the Queen Charlotte Islands.

Winters on Pacific Coast and in interior from Washington (Port Angeles) south to Baja California (Casa Pintada and Ensenada) and Jalisco (October record at Jonila), east to Idaho (Moscow), Texas (San Antonio, Langtry, Brewster County, Fort Clark, mouth of Pecos River), occasionally to North Carolina (Asheville), Georgia (De Kalb County), and northeastern Mexico (Monterrey and Rodrigues, Nuevo Leon).

Exceptions to the general color trend in coastal Alaska were noted in one June and two July specimens from Yakutat that were darker and more grayish above than the general mode. They were quite similar in color to breeding specimens from the Cascade Mountains, being only slightly darker. A specimen taken May 11 on Chichagof Island, Hoonah Sound, and one taken May 2 on Lemesurier Island, Icy Strait, Alaska, look like the dark gray Yakutat Bay population and possibly are migrants. Breeding specimens from Chichagof Island look like other medium olive-brown breeding birds from coastal Alaska.

There is general agreement in the literature, including Ridgway (1907), Hellmayr (1934), and the American Ornithologists' Union (1957), that the name *guttatus,* originally applied to the birds of Kodiak Island, Alaska, is applicable to the population of Alaska in general and southward in a rather indefinite pattern into British Columbia, or even as far as northwestern United States (Miller et al., 1957; Phillips, 1962), excluding the coastal islands of southeastern Alaska

TABLE 2.—*Comparisons of male mean wing lengths among subspecies of* Catharus guttatus (X=means are different at the five percent level of significance or less)

Subspecies	Average wing length (mm)	Number of birds	slevini	nanus	guttatus	vaccinius	oromelus	crymophilus	euborius	faxoni	sequoiensis	auduboni
slevini	84.8	11		X	X	X	X	X	X	X	X	X
nanus	87.9	6	X				X	X	X	X	X	X
guttatus	88.5	12	X				X	X	X	X	X	X
vaccinius	90.0	6	X						X	X	X	X
oromelus	91.6	23	X	X	X				X	X	X	X
crymophilus	92.1	32	X	X	X				X	X	X	X
euborius	93.4	21	X	X	X	X	X	X			X	X
faxoni	93.5	55	X	X	X	X	X	X			X	X
sequoiensis	96.4	15	X	X	X	X	X	X	X	X		X
auduboni	101.6	43	X	X	X	X	X	X	X	X	X	

TABLE 3.—*Comparisons of female mean wing lengths among subspecies of* Catharus guttatus (X=means are different at the five percent level of significance or less)

Subspecies	Average wing length (mm)	Number of birds	slevini	guttatus	nanus	crymophilus	oromelus	faxoni	vaccinius	euborius	sequoiensis	auduboni
slevini	81.7	6		X	X	X	X	X	X	X	X	X
guttatus	84.2	11	X			X	X	X	X	X	X	X
nanus	85.1	9	X			X	X	X	X	X	X	X
crymophilus	88.3	18	X	X	X					X	X	X
oromelus	88.9	15	X	X	X						X	X
faxoni	89.2	21	X	X	X						X	X
vaccinius	89.4	4	X	X	X							X
euborius	91.2	8	X	X	X	X						X
sequoiensis	92.5	6	X	X	X	X	X	X				X
auduboni	97.2	24	X	X	X	X	X	X	X	X	X	

TABLE 4.—*Comparisons of male mean culmen lengths among subspecies of* Catharus guttatus (X=means are different at the five percent level of significance or less)

Subspecies	Average culmen length (mm)	Number of birds	guttatus	nanus	vaccinius	euborius	oromelus	faxoni	crymophilus	auduboni	sequoiensis	slevini
guttatus	12.3	12				X	X	X	X	X	X	X
nanus	12.5	6						X	X	X	X	X
vaccinius	12.8	6						X	X	X	X	X
euborius	13.0	20	X					X	X	X	X	X
oromelus	13.2	24	X					X	X	X	X	X
faxoni	13.6	51	X	X	X	X	X				X	X
crymophilus	13.8	32	X	X	X	X	X					
auduboni	14.0	45	X	X	X	X	X					
sequoiensis	14.1	15	X	X	X	X	X	X				
slevini	14.2	11	X	X	X	X	X	X				

TABLE 5.—*Comparisons of female mean culmen lengths among subspecies of* Catharus guttatus (X=means are different at the five percent level of significance or less)

Subspecies	Average culmen length (mm.)	Number of birds	guttatus	euborius	nanus	oromelus	vaccinius	sequoiensis	crymophilus	faxoni	auduboni	slevini
guttatus	12.2	11			X	X	X	X	X	X	X	X
euborius	12.2	8			X	X	X	X	X	X	X	X
nanus	12.9	9	X	X				X	X	X	X	X
oromelus	13.1	15	X	X				X	X	X	X	X
vaccinius	13.1	4	X	X							X	X
sequoiensis	13.8	6	X	X	X	X					X	X
crymophilus	13.8	18	X	X	X	X					X	X
faxoni	13.8	19	X	X	X	X					X	X
auduboni	14.4	23	X	X	X	X	X	X	X	X		
slevini	14.9	6	X	X	X	X	X	X	X	X		

TABLE 6.—*Comparisons of male mean tarsus lengths among subspecies of* Catharus guttatus (X=means are different at the five percent level of significance or less)

Subspecies	Average tarsus length (mm)	Number of birds	slevini	oromelus	vaccinius	sequoiensis	nanus	guttatus	euborius	auduboni	faxoni	crymophilus
slevini	27.7	11				X	X	X	X	X	X	X
oromelus	27.8	24				X	X	X	X	X	X	X
vaccinius	27.9	6								X	X	X
sequoiensis	28.6	15	X	X						X	X	X
nanus	28.7	6	X	X						X	X	X
guttatus	28.7	12	X	X						X	X	X
euborius	28.8	21	X	X						X	X	X
auduboni	29.4	45	X	X	X	X	X	X	X			X
faxoni	29.7	55	X	X	X	X	X	X	X			X
crymophilus	30.6	32	X	X	X	X	X	X	X	X	X	

TABLE 7.—*Comparisons of female mean tarsus lengths among subspecies of* Catharus guttatus (X=means are different at the five percent level of significance or less)

Subspecies	Average tarsus length (mm)	Number of birds	slevini	oromelus	euborius	nanus	guttatus	vaccinius	sequoiensis	auduboni	faxoni	crymophilus
slevini	26.9	6				X	X	X	X	X	X	X
oromelus	27.1	16				X	X	X	X	X	X	X
euborius	27.8	8							X	X	X	X
nanus	28.3	9	X	X							X	X
guttatus	28.3	11	X	X							X	X
vaccinius	28.4	4	X	X							X	X
sequoiensis	28.7	6	X	X	X						X	X
auduboni	28.7	24	X	X	X						X	X
faxoni	29.3	22	X	X	X	X	X	X	X	X		X
crymophilus	30.4	17	X	X	X	X	X	X	X	X	X	

TABLE 8.—*Gradation of* Catharus guttatus *subspecies by size and color* (reading from top or bottom)

longest wing	*longest bill*	*longest tarsus*
auduboni	slevini	crymophilus
sequoiensis	sequoiensis	faxoni
faxoni	auduboni	auduboni
euborius	crymophilus	euborius
crymophilus	faxoni	guttatus
oromelus	oromelus	nanus
vaccinius	euborius	sequoiensis
guttatus	vaccinius	vaccinius
nanus	nanus	oromelus
slevini	guttatus	slevini
shortest wing	*shortest bill*	*shortest tarsus*
longest tail	*darkest*	*most rufescent*
auduboni	vaccinius	faxoni
sequoiensis	nanus	crymophilus
euborius	crymophilus	nanus
crymophilus	guttatus	euborius
faxoni	oromelus	slevini
oromelus	faxoni	sequoiensis
vaccinius	auduboni	auduboni
nanus	sequoiensis	guttatus
guttatus	slevini	vaccinius
slevini	euborius	oromelus
shortest tail	*palest*	*most grayish*

and British Columbia. The present study indicates a more restricted distribution of this population, to which the name *guttatus* applies, to the vicinity of the coast in Alaska and southward, excluding the outer islands, to middle coastal British Columbia. The southern limit of *guttatus* in that area is indicated by specimens of this race from Yale Lake, Swanson Bay, head of Kukshua Pass, Calvert Island, Canoona River near Graham Reach, Princess Royal Island, and Aristazabal Island.

2. DWARF HERMIT THRUSH: *Catharus guttatus nanus* (Audubon).—Dark, Raw Umber to Prout's Brown. Small: ♂ (6 specimens), wing 85–90 (87.9), tail 62–70 (66.3), culmen 11.5–13 (12.5), tarsus 27.5–30 (28.7), midtoe 15.5–17.5 (16.8); ♀ (9 specimens), wing 83–87.5 (85.1), tail 61–65.5 (63.2), culmen 12–13.5 (12.9), tarsus 27–30 (28.3), midtoe 15–18 (16.7).

Darker and more rufescent than *guttatus*; more rufescent than *vaccinius*; smaller and flanks more grayish than *crymophilus*; more rufescent and shorter wing and tarsus than *oromelus*; much darker, shorter bill, and longer wing than *slevini*.

Breeds on the outer islands of the Alexander Archipelago in southeastern Alaska and the Queen Charlotte Islands of British Columbia.

Winters on the Pacific Coast from southwestern British Columbia (Victoria) south to California (Humboldt Bay).

Osgood (1901) accurately described the hermit thrush population of the Queen Charlotte Islands, distinguishing it from that of the coast of southern Alaska, and named these dark, rufescent birds "*Hylocichla guttata verecunda*." In so doing he disposed of the name *nanus* Audubon (1839) by referring it to the eastern population. He did this chiefly on the grounds that Audubon's (1838) folio plate, on which the original description of *nanus* was based, showed a bird with "brown sides," a characteristic considered by Osgood to be restricted entirely to eastern birds. This view has been supported by Phillips (1962).

In the course of the present study, I have compared both fresh and worn plumaged hermit thrush specimens representing different recognizable populations with Fig. 1, Plate 419, of Audubon's (1838) folio edition, which depicts the "Little Tawny Thrush, *Turdus minor*, Gmelin" that Audubon (1839) later said represented his newly described "*Turdus Nanus*." The plate I used, which is in the set of Audubon's folio in the library of the Smithsonian Institution, shows a relatively dark brown-backed hermit thrush with fairly dark gray flanks tinged with buff, not the light grayish buffy characteristic of eastern populations. Of the specimens used in the comparison, it matches most closely in color those from the Queen Charlotte

Islands. In fresh plumage these have a distinct buffy wash on the relatively dark gray flanks. The small size, particularly the bill, which was stressed by Audubon (1839) in his description of *nanus*, also would seem to eliminate all except the small western races, and of these the only one with a buffy tinge to the flanks is the Queen Charlotte Island population. Audubon said that the haunts of his newly described *nanus* were the valleys of the Columbia River whence he had obtained it through Dr. Townsend. This further indicates the probability that the description of *nanus* was based on a western specimen. Audubon mentioned a few very small specimens from eastern localities that he referred to *nanus*. These were probably also representatives of far western populations, although not necessarily the Queen Charlotte Island one, which seems to stick more closely to the Pacific Coast than some of the other small hermit thrushes such as *guttatus* and *oromelus*. Specimens of both these races from the Atlantic seaboard have been seen in connection with the present study, but neither has any buffy tinge to the flanks and so could not have been the basis for Audubon's plate.

Since there is some question (see Phillips, 1962) about the authenticity of the presumed type-specimen of *nanus* designated by Brewster (1902) and located in the Museum of Comparative Zoology at Harvard, it seems prudent to rely most heavily on Audubon's original description and the illustration that was mentioned in it. On the basis of these, I believe the correct course is that set by Ridgway (1907), Hellmayr (1934), and many others in assigning the name *nanus* to the Queen Charlotte Island population on the basis of Audubon's description of a migrant specimen taken near the lower Columbia River.

Ridgway (1907) seems to have correctly distinguished the distribution of *nanus* from that of *guttatus* in Alaska, with the former restricted to the Queen Charlotte Islands and the outer islands of the Alexander Archipelago. Specimens examined in the present study, however, indicate that his postulated extension of the range of *nanus* southward to include the coast of British Columbia and Washington is without basis.

Munro and Cowan (1947) noted that the population of the Queen Charlotte Islands is typical *nanus* and, although extending its range south to the mountains of the Vancouver region, noted that the population of that area exhibits characters of the inland race, *oromelus*. This accords with findings in the present study but, unlike Munro and Cowan, I consider the populations of southwestern British Columbia too different from the Queen Charlotte birds to include under the name *nanus*, and I have included them under *vaccinius*.

3. VANCOUVER HERMIT THRUSH: *Catharus guttatus vaccinius* (Cumming).—Dark, Brownish Olive. Small: ♂ (6 specimens), wing 86.5–93. 5 (90), tail 64–69.5 (66.9), culmen 12.5–13 (12.8), tarsus 27–29 (27.9), midtoe 15–16.5 (15.7); ♀ (4 specimens), wing 86.5–90.5 (89.4), tail 66–68.5 (67.3), culmen 12.5–14 (13.1), tarsus 27–30 (28.4), midtoe 16–17 (16.3).

Darker and longer tarsus than *oromelus;* longer wing, shorter bill, and darker than *slevini;* more grayish than *nanus;* darker than *guttatus.*

Breeds on Vancouver Island, British Columbia, and in a very limited area on the mainland near Vancouver.

Winters on Pacific Coast from southwestern British Columbia (Victoria) south to California (Pasadena). Eastward in migration to Idaho (Moscow) and New Mexico (Mogollon Mountains).

Swarth (1912) first suggested the distinctness of a dark Vancouver Island population on the basis of six juvenile specimens, and Cumming (1933) accurately described it as a separate subspecies giving it the name *"vaccinia."* There is no indication in either the original description of *vaccinius* or in the present study of a smaller size among breeding specimens from Vancouver Island as compared with the breeding examples from coastal areas farther north mentioned by McCabe and McCabe (1932). If anything, Vancouver Island specimens are larger than more northern coastal birds. Since the original description, most investigators seem to have overlooked the distinctive characters of this race and have usually incorporated the Vancouver Island population under *nanus* (=*verecundus*). Munro and Cowan (1947), the American Ornithologists' Union (1957), Phillips (1962), and Ripley (1964) followed this course. The main character distinguishing *vaccinius* from *nanus* is the more grayish or sooty (less reddish) brown coloration of the upperparts. Munro and Cowan (1947) described specimens from the "mainland coast adjacent to Vancouver" as appearing to share the characters of both *nanus* and *oromelus,* but included the specimens under the former name. The present writer, in Jewett et al. (1953), recognized the distinctness of the dark relatively grayish Vancouver Island race but made the error of incorporating northern Washington State and adjoining portions of British Columbia within its range. It appears from the present study that the very dark characters of *vaccinius* do not apply extensively to mainland populations although birds occupying a mountain habitat adjacent to Vancouver are included herein in the range of *vaccinius* on the basis of characters noted by Munro and Cowan (1947).

4. MONTEREY HERMIT THRUSH: *Catharus guttatus slevini* (Grinnell).—Pale, Light Brownish Olive, sparsely spotted below. Shortest wing, long bill: ♂ (11 specimens), wing 82–88.5 (84.8), tail

59–67 (64.1), culmen 12.5–15.5 (14.2), tarsus 27–28.5 (27.7), midtoe 14.5–16 (15.1); ♀ (6 specimens), wing 78–84 (81.7), tail 57–63.5 (60.4), culmen 14.5–16 (14.9), tarsus 26–28 (26.9), midtoe 15.5–16 (15.6).

Shorter wing, longer bill, paler above and more sparsely spotted below than *oromelus*, *vaccinius*, *nannus*, and *guttatus;* much smaller wing and tarsus than *sequoiensis*, but color and bill length similar; smaller wing and tarsus and longer bill than *euborius*.

Breeds locally in coastal areas of California, Oregon, and Washington State.

Winters in Baja California (Mt. Miraflores, El Sauz, Laguna, and Cape San Lucas); probably also in other portions of southwestern United States and northwestern Mexico (Phillips et al., 1964). Eastward in migration to Texas (Leon Springs, El Paso, and San Antonio).

Grinnell's (1901) original description accurately portrays the characters of this very small, pale coastal subspecies although the distribution he gave is more limited than is actually the case. McCabe and McCabe (1933, map, p. 123) seem to have been the first to suggest the northward extension of the range of *slevini* from California along the Pacific coastal mountains of Oregon and Washington. Examination of specimens in the present study shows this to be correct. The birds with characters of *slevini*, although not in typical form, range northward to the west of the Cascade Mountains as far as the Olympic Peninsula of northwestern Washington, but the breeding distribution appears to be interrupted considerably in Oregon and Washington. Specimens from the west slopes of the Cascades in this general area are intermediate between *slevini* and *oromelus*. They are lighter and more rufescent above than typical *oromelus* of the eastern slopes of the Cascades, northern Idaho, and southern British Columbia, and in this respect are like *slevini*. The specimens are intermediate in size and ventral spotting between these two races.

The abrupt transition from the pale, Light Brownish Olive *slevini*-type of coloration found on the Olympic Peninsula of Washington to the dark, Brownish Olive *vaccinius* on Vancouver Island across the Straits of Juan de Fuca is rather surprising and, together with the very disrupted range in coastal areas of Oregon and Washington, suggests a relatively recent occupation of the Olympic Peninsula by extension of the range from the south.

The hermit thrush population of the Olympic Peninsula has been described as a distinct subspecies (*jewetti*) by Phillips (1962) on the basis of darker and more reddish brown coloration above and heavier spotting below than *slevini* of California. The present study has verified the difference from both *slevini* and *oromelus* of specimens

from the Olympic Peninsula noted by Phillips, as well as of similarly colored specimens from the west slopes of the Cascades. These differences, however, seem to be better treated as indicating populations intermediate in both size and color between the races *slevini* and *oromelus*, with those closer to the coast being nearer *slevini* and those closer to the Cascade divide nearer to *oromelus*.

5. SIERRA HERMIT THRUSH: *Catharus guttatus sequoiensis* (Belding).—Pale, Light Brownish Olive. Medium sized: ♂ (15 specimens), wing 93–100 (96.4), tail 67–75 (70.8), culmen 13–15 (14.1), tarsus 27–30 (28.6), midtoe 15–18.5 (16.8); ♀ (6 specimens), wing 90–95 (92.5), tail 64–73 (68.8), culmen 13–14.5 (13.8), tarsus 28–30 (28.7), midtoe 15–17.5 (16.4).

Shorter wing and tarsus than *auduboni;* longer wing than *slevini, nanus*, and *guttatus;* larger, paler, and more rufescent than *oromelus* and *vaccinius;* longer bill than *euborius;* more grayish and shorter tarsus than *faxoni* and *crymophilus*.

Breeds in the Sierra Nevada, Mount Pinos, and San Bernardino Mountains of California.

Winters in Mexico (Baja California and Monterrey, Nuevo Leon) south to Guatemala (Hacienda Chancol, also May 1 at Chemal).

McCabe and McCabe (1933) and the American Orinthologists' Union (1957) have correctly limited the northward extension of the population to which the name *sequoiensis* applies to the Sierra Nevada of California. Other populations to the north of California, even as far as the Yukon River in Northwest Territory, have been referred to *sequoiensis* by Ridgway (1907), Brooks and Swarth (1925), Gabrielson and Jewett (1940), Rand (1948), and Phillips (1962). These populations, however, appear to be referable to other races or are intermediate between these (see accounts under *auduboni* and *euborius*).

6. AUDUBON'S HERMIT THRUSH: *Catharus guttatus auduboni* (Baird).—Pale, Light Brownish Olive. Largest: ♂ (45 specimens), wing 94–111 (101.6), tail 66.5–79 (73.5), culmen 13–15.5 (14.0), tarsus 27–31.5 (29.4), midtoe 15.5–19.5 (17.3); ♀ (24 specimens), wing 92.5–101 (97.2), tail 66–74 (70.0), culmen 13–15.5 (14.4), tarsus 26.5–30.5 (28.7), midtoe 15.5–19 (17.0).

Longer wing and tarsus but similar in color to *sequoiensis* and *euborius;* larger and more grayish than *crymophilus* and *faxoni;* much larger and more rufescent than *oromelus* and *vaccinius;* much larger than *guttatus* and *nanus*.

Breeds in the mountains of the Great Basin and Rocky Mountains from southeastern Washington, middle Idaho, southeastern British Columbia, and southwestern Alberta south almost to the Mexican border.

Winters in Mexico (Sonora, Chihuahua, Guerero, Michoacan, Morelos, Vera Cruz), south to Guatemala (Hacienda Chancol).

Populations breeding in northwestern Montana, extreme southeastern British Columbia, and southwestern Alberta that have been referred to *sequoiensis* by various authors, including Ridgway (1907), Rand (1948), and Phillips (1962), probably are better considered as intermediates between the large *auduboni*, to which race it is assigned, and smaller races to the west, north, and east. Migrant specimens from this region very likely are responsible for some of the more eastern literature records of "*sequoiensis*," which race they resemble superficially.

As McCabe and McCabe (1932) pointed out, there is a tendency for specimens with largest measurements to be from the southern and middle Rocky Mountain area. For that reason, these authors, as well as other investigators, recognized the distinctness of a Great Basin race named "*polionota*" by Grinnell (1918) on the basis of breeding birds taken in the White Mountains in central eastern California. In the present study, I was unable with any degree of certainty to sort out specimens on the basis of either size or color as belonging to either a Great Basin or a Rocky Mountain race. Larger and smaller as well as more grayish and more rufescent specimens seemed completely intermingled even at the type-locality of *polionota* in the White Mountains. If segregation into discrete breeding populations with different combinations of morphological characters exists, it must be quite local and possibly correlated with local ecological differences of the sort reported for hermit thrushes in Colorado by Packard (1945) or as postulated for nighthawks by Selander (1954). Such segregation was not apparent in the information furnished by specimens examined in the present study; therefore, I am taking the course followed by Phillips (1962) and considering *polionota* a synonym of *auduboni* and applying that name to the entire Rocky Mountain-Great Basin complex of large, pale hermit thrushes.

7. Cascade hermit thrush: *Catharus guttatus oromelus* (Oberholser).—Medium shade, most grayish, Olive. Small: ♂ (24 specimens), wing 89.5–94.5 (91.6), tail 58–73 (68.0), culmen 11.5–14.5 (13.2), tarsus 26.5–31.5 (27.8), midtoe 15–18 (16.8); ♀ (16 specimens), wing 86–96 (88.9), tail 62–74 (66. 5), culmen 12–13.5 (13.1), tarsus 25.5–29 (27.1), midtoe 15.5–18 (16.8).

Longer wing and shorter bill, darker and more grayish than *slevini;* longer wing and bill, shorter tarsus, and more grayish than *guttatus;* shorter tarsus, paler and more grayish than *nanus;* paler than *vaccinius;* shorter wing, darker and more grayish than *sequoiensis* and *euborius.*

Breeds on the mainland of southern British Columbia south to northern Idaho and northern Washington, and in the Cascade Mountains south to extreme northern California.

Winters on Pacific Coast of southern California (Los Angeles County), east to Texas (Langtry and Frijole), and occasionally to North Carolina (Asheville), south to northeastern Mexico (Monterrey, Nuevo Leon, and Victoria, Tamaulipas).

McCabe and McCabe (1932) apparently were the first to point out the distinctive characters of the small, grayish hermit thrushes breeding in southern British Columbia, northern Washington, and northern Idaho but did not assign a name to them. They did not at that time have material to show the extension of the characters southward in the Cascades to northern California. Oberholser (1932) described the distinct characteristics of the birds from the Warner Mountains of southern Oregon and the Cascades and noted that these characteristics were shared by birds from central-southern British Columbia. He named this subspecies "*oromela.*" With additional material, McCabe and McCabe (1933, map) completed the picture of distribution of races of hermit thrushes in the northwestern United States and assigned the Cascades and northern Idaho, along with southern British Columbia, to the race *oromelus*. This arrangement agrees with findings in the present study. Later, Bishop (1933) described the small gray population occupying part of the range of *oromelus* in northern Idaho, naming it "*dwighti.*" Although Ripley (1964) includes this in the synonomy of *auduboni*, the present study indicates that it is a synonym of *oromelus*.

Munro and Cowan (1947) further confirm the distinctness of *oromelus* in southern British Columbia and define its distribution there more precisely. Their findings agree with those of the present study, except that they apparently lacked specimens at the time which showed the westward extension of *oromelus* characters to the vicinity of the Pacific Coast north of Vancouver Island.

Doubt has been cast on the applicability of the name *oromelus* to the population in question because of the selection of the type-specimen from the Warner Mountains of central-southern Oregon, a locality at the extreme southern end of the range of this subpsecies. McCabe and McCabe (1933) and Miller (1941a) pointed out the intermediacy of the Warner Mountains birds between those from farther north in the Cascades and *slevini* of the California coast; and, although they had not seen the type-specimen of *oromelus*, they questioned the use of this name for the more northern population. Ripley (1964) considers *oromelus* a synonym of *slevini*. Both Phillips (1962) and the present writer, after correspondence with Robert Storer and the late Josselyn Van Tyne of the Museum of

Zoology at the University of Michigan, are convinced that the type-specimen of *oromelus*, which is in that museum, is in fact a representative of the Cascade race. Van Tyne (in litt., 1955) reported that he had compared the type, an immature male, with two breeding male specimens I had sent him, one typical of the Cascade race and the other typical *slevini*, and found that it was closer in color to the former. The measurements of the type of *oromelus* (wing 93 mm, tail 72, exposed clumen 13, tarsus 29.5, and midtoe 15) are typical of the Cascade and southern British Columbia population and quite unlike those of *slevini*. For indication of intergradation between *oromelus* and *slevini* in western Oregon and Washington, see the account under *slevini* (no. 4).

8. YUKON HERMIT THRUSH: *Catharus guttatus euborius* (Oberholser).—Pale, Light Brownish Olive. Medium sized, small billed: ♂ (21 specimens), wing 89–97.5 (93.4), tail 65–73.5 (69.2), culmen 12–14 (13.0), tarsus 26.5–30 (28.8), midtoe 16.5–18.5 (17.3); ♀ (8 specimens), wing 87.5–97.5 (91.2), tail 65–75 (68.9), culmen 10.5–13 (12.2), tarsus 25.5–30 (27.8), midtoe 14.5–18.5 (16.2).

Longer wing, paler and more rufescent than *guttatus* and *vaccinius;* longer wing and tarsus, paler and more rufescent than *oromelus;* shorter tarsus and more grayish than *faxoni* and *crymophilus;* shorter wing and bill than *sequoiensis* and *auduboni.*

Breeds from central Alaska southeastward through southern Yukon to central British Columbia and southwestern and south-central Alberta.

Winters from Arizona (Santa Rita Mountains) and western Texas (Brewster County and mouth of Pecos River) south to northeastern Mexico (Rodriguez and Monterrey, Nuevo Leon). In migration east to Illinois (Glenwood), Mississippi (Saucier), and Georgia (Jeffersonville).

The original description of *euborius* (Oberholser, 1956) fits the characteristics of this population very well. The original range given also falls entirely within the more extensive area in which the characters were found to occur in the present study.

This population has been included by earlier authors, such as Ridgway (1907), Gabrielson and Jewett (1940), and Rand (1948), within the range of *sequoiensis*. More recently, however, most authors have considered the birds of this area referable to *guttatus* (Munro and Cowan, 1947; Brooks and Swarth, 1925; the American Ornithologists' Union, 1957; and Ripley, 1964).

Phillips (1962), after rejecting the name *euborius* because he considered the type-specimen too worn for certain identification but probably referable to the eastern hermit thrush "*nanus*" (=*faxoni*), proceeded to describe as a distinct subspecies the breeding birds of the central and northern interior of British Columbia and named the

subspecies "*munroi*." Ripley (1964) has considered this name a synonym of *nanus* but, according to the present study, both the type-locality of *munroi* (Nulki Lake in central British Columbia) and that of *euborius* (Lewes River in south-central Yukon) are in the range of hermit thrushes having similar morphological characters quite different from coastal birds. Also, since the original description of *munroi* and a specimen taken at Nulki Lake on May 18, examined in the present study, fit well with the characters of this population, it appears that *munroi* must be considered a synonym of *euborius*, the older name.

Two specimens taken on May 20 and one in May without specific date at Fairbanks, Alaska, have characters that fit *euborius*. Although these specimens probably were not breeding at that time, on the probability that they would nest in that general area, the range of *euborius* is considered to extend northwestward to that point on the Tanana River in central Alaska.

Breeding specimens from Tupper Creek and Charlie Lake in northeastern British Columbia, also Banff, Jasper Park, and Grimshaw in southern Alberta, are somewhat intermediate toward *faxoni*, but are closer to *euborius* in pale coloration and grayishness of flanks. Other investigators, including Munro and Cowan (1947) and Rand (1948), have assigned specimens from these same areas to *faxoni*. These facts indicate that the area of intergradation between *euborius* and *faxoni* is a broad one in those regions.

9. EASTERN HERMIT THRUSH: *Catharus guttatus faxoni* (Bangs and Penard).—Medium shade, Saccardo's Umber to Cinnamon Brown. Medium size, long tarsus; ♂ (55 specimens), wing 89–100 (93.5), tail 64–79 (68.5), culmen 12.5–15 (13.6), tarsus 28–32.3 (29.7), midtoe 15–18.5 (17.2); ♀ (22 specimens), wing 84–94.5 (89.2), tail 60–70 (65.0), culmen 13–15 (13.8), tarsus 27.5–31 (29.3), midtoe 15–19 (16.9).

Longer bill and tarsus, darker and more rufescent than *euborius;* shorter wing, longer tarsus, and more rufescent than *auduboni* and *sequoiensis;* paler than *crymophilus;* larger and more rufescent than *oromelus*, *vaccinius*, and *guttatus;* larger, paler and more rufescent than *nanus*.

Breeds from south-central Mackenzie, extreme northeastern British Columbia (?), and central-eastern Alberta east to central-western Quebec, Nova Scotia, southeastern New York, and the northern Appalachian Mountains.

Winters in eastern and central-southern United States from New York State (Highland Falls) south to Florida (Jacksonville and Enterprise) and west to Oklahoma (Tulsa) and Texas (San Antonio, Hidalgo, Navasota, and Fort Clark).

Bangs and Penard (1921), after considering the confusion in the literature relating to the name of the eastern hermit thrushes, concluded that no name that had been proposed could with certainty be considered as referring to that population. They therefore described and named it *"faxoni"* on the basis of an adult breeding specimen from Shelburne, N.H. Most authorities, including the American Ornithologists' Union (1957), have used this name ever since. Phillips (1962), as noted above, has renewed the old controversy over the applicability to the eastern hermit thrush population of Audubon's *nanus*. The evidence, however, seems to support the conclusion that Audubon (1839) used the name *nanus* to refer to a small far-western form. Under the circumstances I prefer to follow well-established current usage and apply the name *faxoni* to the eastern population, which embraces the New Hampshire birds from which the type-specimen was selected. This includes all breeding hermit thrushes, with virtually no geographical variation, from the vicinity of Great Slave Lake southeastward to Nova Scotia and Long Island, N.Y. Breeding birds from the latter locality apparently were examined for the first time in the present study. Specimens from western Mackenzie (Hay River, Fort Providence, and Fort Resolution) are somewhat intermediate toward *euborius* in possessing more grayish flanks and slightly paler and more grayish coloration above than breeding birds from the Appalachian Mountains and New England, but in both respects they are closer to the eastern specimens.

10. NEWFOUNDLAND HERMIT THRUSH: *Catharus guttatus crymophilus* (Burleigh and Peters).—Dark Brownish Olive to Prout's Brown. Medium size, long tarsus: ♂ (33 specimens), wing 87–98.5 (92.1), tail 65–75.5 (69.2), culmen 13–14.5 (13.8), tarsus 29.1–32 (30.6), midtoe 15.5–19.5 (17.6); ♀ (18 specimens), wing 84–94 (88.3), tail 62–71.5 (66.5), culmen 13–15 (13.8), tarsus 28.6–32.5 (30.4), midtoe 15.5–19.5 (17.3).

Darker than *faxoni;* larger and more rufescent on flanks than *nanus;* longer tarsus, shorter wing, darker and more rufescent than *auduboni, sequoiensis,* and *euborius;* longer tarsus, darker and more rufescent than *guttatus, vaccinius,* and *oromelus.*

Breeds from James Bay in central-western Quebec east to southern Labrador, Newfoundland, and Cape Breton Island, Nova Scotia.

Winters in southeastern, central and central-southern United States from Maryland (Elliot Island, Shadyside, Leonardstown, Port Tobacco, and Powellville), south to Florida (Kissimmee) and west occasionally to central Colorado (one record, west Denver) and central-southern Texas (San Antonio, Sinton, and Harlingen).

The original description of *C. g. crymophilus* by Burleigh and Peters (1948), depicting it as darker above than *faxoni* of the eastern

United States, also accurately describes breeding populations of a considerably greater area of eastern Canada northeast of the range of *faxoni*.

All eastern populations of the hermit thrush have distinct color phases—rufescent and grayish—and it is important to sort specimens into their respective phase groups before comparisons for identification are attempted. Compared with each other, phase with phase, plumage of the upper parts of breeding specimens from southern Quebec, New England, and the Appalachian Mountains shows a paler shade than that of birds from farther north in Quebec and Newfoundland. Specimens from the mainland of Labrador and Quebec are somewhat more greenish, less brownish than Newfoundland birds, but are closer to them than to *faxoni*.

Breeding specimens from northern Maine, eastern New Brunswick, and Prince Edward Island are intermediate between *faxoni* and *crymophilus* but closer to the former, while those from Cape Breton Island of extreme northeastern Nova Scotia are referable to *crymophilus*.

Summary

The hermit thrush, *Catharus guttatus*, is distributed widely on the North American continent, breeding in seven different ecological climax zones or "Life Areas," and wintering mostly south of these areas in the southern United States, Mexico, and Guatemala.

Females are smaller in wing but proportionately larger in bill measurements than males; there are no color differences correlated with sex.

Young birds may carry a few recognizable juvenal wing coverts until their first postnuptial molt.

There are two slightly differentiated color phases.

There are marked geographical differences in color, size, and proportion among hermit thrushes.

The greatest geographically correlated variation occurs west of the Rocky Mountains.

The smallest birds, except for bill, breed in the vicinity of the Pacific Coast; the largest in the middle and southern Rockies.

The population with the longest bill and the shortest wing breeds near the California coast.

Eastern populations are medium sized but have the longest legs.

Relatively rufescent coloration is associated with more northern and eastern distribution; relatively grayish coloration with more southern coastal and interior mountain areas of the west. Darkest tones are associated with the northern Pacific coastal islands and

extreme northeast, palest with more southern Pacific Coast and interior mountains.

Color variation seems to be correlated at least in part with environmental moisture of the breeding areas (Gloger's law), but there are a few exceptions.

Body mass, as indicated by wing length, and length of appendages are correlated with temperature in accordance with Bergmann's and Allen's laws, respectively, in some breeding areas but not in others.

Failure of certain populations to conform to these laws of geographical variation with respect to breeding distribution may be explained in some cases by adaptation to environments in wintering areas.

Adaptation to environmental conditions appears to be more important in producing morphological variation in populations than physiographical or ecological barriers to gene flow.

Regional trends toward dark pigmentation associated with moist climate may be enhanced by physical isolation on offshore islands.

The hermit thrush and others recently included in the genus *Hylocichla*, excepting the woodthrush, are better classified on the basis of morphology and behavior in the genus *Catharus*.

Populations of hermit thrushes grouped by morphological, ecological, and geographic characteristics break up into 10 recognizable groups that may be considered as distinct races or subspecies; all of these have previously supplied names.

Each named subspecies is characterized as to color, size, breeding distribution, and winter distribution; and the history of its characterization and nomenclature are discussed.

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